

The phyletic position of the Ad Dabtiyah hominoid

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Synopsis

The hominoid maxilla and four isolated teeth from Ad Dabtiyah, Saudi Arabia, are assigned here to a new genus and species *Heliopithecus leakeyi*. It shares numerous primitive characters with *Proconsul* (for example, molar cingula and premolar cusp heteromorphy), and a few advanced characters with *Kenyapithecus* (for example premolar enlargement and molar enamel thickening). The latter characters are also characteristic of the great ape and human clade, and for this reason it is grouped with that clade, but it is a more primitive member than *Kenyapithecus* because it retains more primitive characters. Molar enamel is intermediate in thickness and all pattern 3, the first hominoid so far described to have this combination, and this places it intermediate between gibbons and *Proconsul* which have thin pattern 3 enamel, and *Kenyapithecus* and the ancestral great ape and human morphotype which have thick pattern 3 enamel.

Introduction

We describe here a new genus and species of hominoid primate from continental equivalents of the basal deposits of the marine Dam Formation near Ad Dabtiyah, Saudi Arabia: see Whybrow *et al.* (this issue, p. 371). The hominoid specimens from these early middle Miocene deposits were first described by Andrews *et al.* (1978), and the associated fauna and geology were described by Hamilton *et al.* (1978). The hominoids were not named, but were considered to be intermediate in morphology between the early Miocene species of *Proconsul* from east Africa and later Miocene species of *Ramapithecus* and *Sivapithecus* from Eurasia. Comparison was made with the type specimen of what was originally called *Sivapithecus africanus* (Le Gros Clark & Leakey 1950) and subsequently *Kenyapithecus africanus* (Leakey 1967), but the taxonomic position and provenance of this species was too uncertain itself for this comparison to be particularly helpful.

Much progress has been made recently which has improved our ability to determine the phylogenetic status of the hominoid from Ad Dabtiyah. Both the hominoid clade and its constituent clades have now been better defined (Harrison 1982, Andrews 1985, Martin 1986). In particular, work on the structure and thickness of molar enamel has clarified its significance in hominoid evolution (Martin 1983, 1985), and comparisons with Spanish and Hungarian material, all assigned to *Dryopithecus* (Martin & Andrews 1982), have expanded our knowledge of this middle Miocene genus. Some new material is also available for *Kenyapithecus* (Pickford 1982, Ishida *et al.* 1984). The Ad Dabtiyah material is considered to resemble both *Dryopithecus* and *Kenyapithecus* in derived characters and to be linked with them in the great ape and human clade. *Proconsul*, by contrast, cannot be shown to share any derived characters with this clade although it does appear to have some hominoid synapomorphies (Andrews 1985, Fleagle 1986). It is now clear that the Ad Dabtiyah hominoid shares only primitive characters with *Proconsul* and is not therefore uniquely related to it; it would also appear that the characters it shares with *Kenyapithecus* and *Dryopithecus* are synapomorphies of the great ape and human clade and are also not indicative of special relationship. On the contrary, both *Kenyapithecus* and *Dryopithecus* share derived characters with the great apes and humans not present in the

Ad Dabtiyah specimens. For these reasons, we have decided to name a new genus and species for this material while recognizing its taxonomic relationship with *Kenyapithecus* and the great apes and man.

Systematics

Superfamily HOMINOIDEA Simpson 1931

Genus *HELIOPITHECUS* gen. nov.

DIAGNOSIS. A genus of hominoid with the enlarged premolars characteristic of the great ape and human clade; the P³ is elongated with a massive buccal cusp and with great buccal flare, and the P⁴ is also elongated but without the buccal flare; the premolars are large relative to M¹, both in length and breadth, and are comparable to *Kenyapithecus* in this respect; they differ from this genus in the greater cusp heteromorphy of the premolars and the greater cingulum development on the upper molars; the tooth enamel is all pattern 3 and is intermediate in thickness, that is thicker than in *Proconsul* but thinner than in *Kenyapithecus*; the teeth wear with the dentine separation pattern.

NAME. Greek, *Helios*, the sun, and *pithekos*, an ape.

TYPE SPECIES. *Heliopithecus leakeyi* sp. nov.

Heliopithecus leakeyi sp. nov.

HOLOTYPE. M.35145, a slightly crushed maxilla from the left side with the crowns of P³ to M² and the lingual alveolar margins of I² and C. The specimen is housed in the Department of Palaeontology, British Museum (Natural History).

TYPE LOCALITY. Ad Dabtiyah, Saudi Arabia: 4 km south-east of the salt flat named Ad Dabtiyah, 26° 27' 02" N, 48° 35' 24" E.

PARATYPE. M.35146, isolated upper third molar.

REFERRED MATERIAL. Three isolated teeth, M.35147-9.

DIAGNOSIS. As for genus.

NAME. In honour of Louis Leakey, who did so much to add to our knowledge of hominoid evolution.

DESCRIPTION. The descriptions of this fossil hominoid can be added to in three ways from the previous descriptions (Andrews *et al.* 1978): variability within the sample; the significance of premolar enlargement; and changes in enamel thickness. Measurements, see Table 1.

Table 1 Measurements of the teeth of *Heliopithecus leakeyi*. md = mesiodistal length, bl = buccolingual breadth; all measurements in millimetres.

Specimen	md	bl	bl/md	Crown module	Crown height	
					buccal	lingual
P ³ M.35145	7.7	11.6	150.1	9.7	8.4	4.0
P ⁴ M.35145	7.0	11.4	162.8	9.2	5.8	5.4
M.35149	5.3	9.7	183.0	7.5	5.7	4.2
M ¹ M.35145	8.8	10.5	119.3	9.7	—	—
M ² M.35145	9.5	11.9	125.3	10.7	—	—
M ³ M.35146	10.4	12.9	124.0	11.7	—	—
dP ⁴ M.35147	6.9	8.3	120.3	7.6	—	—
dC M.35148	5.9	4.9	83.1	—	5.0	—



Fig. 11 Occlusal view of the type specimen of *Heliopithecus leakeyi* (M.35145). Below right are three of the isolated teeth, from left to right, M.35147, right dP⁴; M.35148, right dC; and M.35149, right P⁴.

Sample variability

It was originally suggested (Andrews *et al.* 1978) that the isolated P⁴ (M.35149) might belong to a separate species from the maxilla M.35145. This is no longer considered likely on the basis of metrical dimensions in comparison with other closely related taxa. For instance, in the genus *Kenyapithecus* we would now combine *K. wickeri* from Fort Ternan and *K. africanus* from Maboko (Andrews & Walker 1976, Pickford 1982) into a single species (Greenfield 1979), and recognize this species as being distinct from the Asian genera *Sivapithecus* and *Ramapithecus* which themselves have now been grouped together (Greenfield 1980, Andrews & Cronin 1982). The metrical and morphological differences in the premolars of the *wickeri* and *africanus* specimens are very similar to those seen in the two specimens from Ad Dabtiyah: for instance the buccolingual variation of the P⁴ is 10.5 to 12.0 mm in the African specimens and 9.7 to 11.4 mm in the Ad Dabtiyah specimens (Fig. 12). Similarly, the ranges in P⁴ buccolingual dimensions for *Proconsul africanus* (from Rusinga only) is 8.5 to 9.9 mm and for *Proconsul nyanzae* is 9.6 to 11.7 mm (Andrews 1978), both similar to the range seen in the Ad Dabtiyah specimens; greater if the Rusinga *africanus* is combined in a single species with the Rusinga *nyanzae*. In comparison with these there is no good reason for not including all the Ad Dabtiyah specimens in the one species *Heliopithecus leakeyi*.

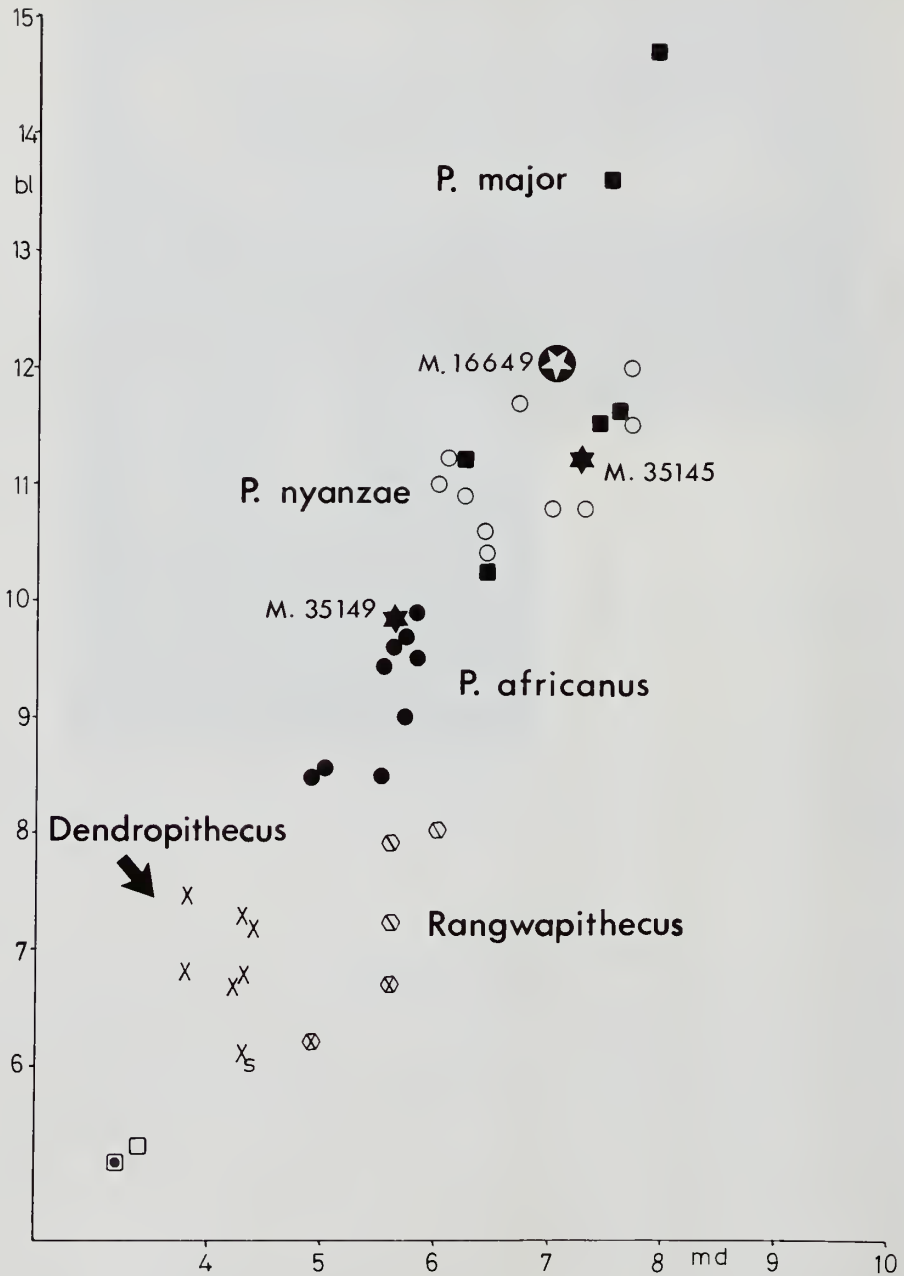


Fig. 12 Size variation of the upper fourth premolar. The two specimens from Ad Dabtiyah (M.35145 & M.35149) are identified by closed stars and the type specimen of *Kenyapithecus africanus* (M.16649) by an open star. The sample ranges of three species of *Proconsul* and two species of *Rangwapithecus* are shown for comparison.

Premolar enlargement

The main characteristic of *Heliopithecus leakeyi* is the great enlargement of the premolars. The P^3 is larger than the P^4 and both are nearly as large as the first molar in cross-sectional area (Andrews *et al.* 1978). Fig. 13 shows this to be an important feature: the extant great apes have a relatively larger P^3 than do most Miocene hominoids, and *Heliopithecus* and *Kenyapithecus* are both within the great ape range and outside the range of other Miocene hominoids. For the P^4 , on the other hand, they differ from both living and fossil apes. They both have unusually large P^4 s, and in this they resemble the palate from Moroto, Uganda, which has previously been incorrectly referred to *Proconsul major* (Pilbeam 1969, Andrews 1978), but which would seem on this evidence to belong either to *Kenyapithecus* or *Heliopithecus*. There is evidence here, therefore, both for the relationship of these two genera based on premolar morphology, and for their relationship with the extant great apes; and it may be that the Moroto palate also belongs with this group. (See Note added in proof, p. 391.)

The premolars and molars of *Heliopithecus* generally have low rounded cusps, the exception being the buccal cusp of P^3 , which is more than twice the height of the lingual cusp. In this latter feature it differs from *Kenyapithecus* and *Dryopithecus* but resembles the Moroto palate, and it would seem likely to be a primitive retention which has been lost in *Kenyapithecus* and

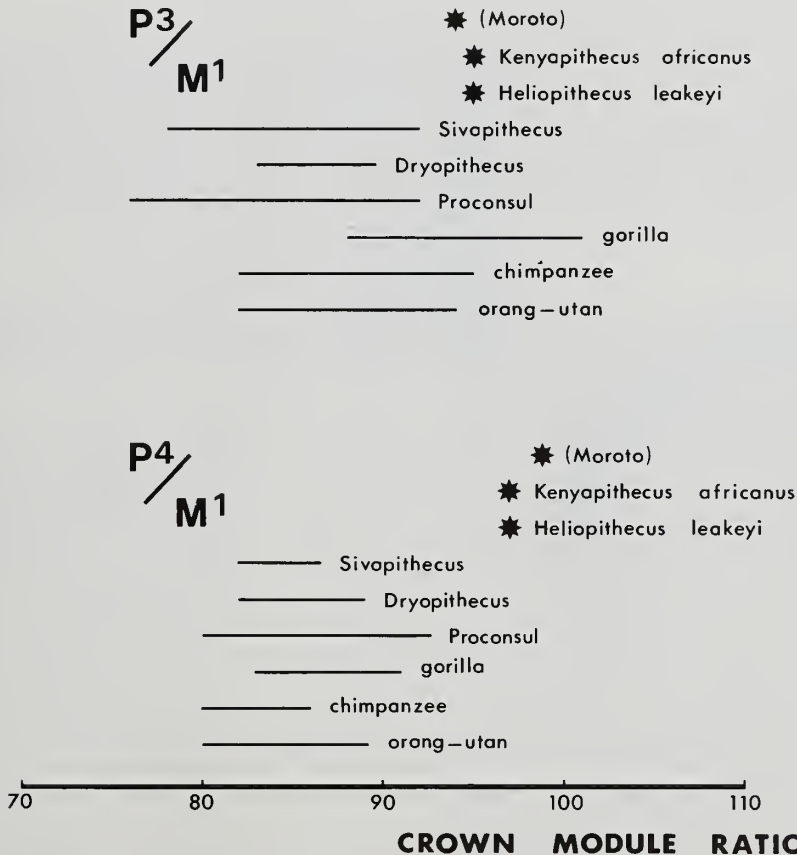


Fig. 13 Size ranges of the third and fourth premolars. The horizontal axis shows the premolar/molar size ratios calculated for the crown modules (length + breadth/2). The total ranges for a number of living and fossil taxa are shown (*Proconsul* = 3 species; *Sivapithecus* = 2 species) for comparison with *Heliopithecus leakeyi*.

Dryopithecus. Other characters of the molars show this same combination, particularly the presence of upper molar and premolar cingula, which have been lost in later Miocene fossil hominoids and in the extant great apes. The type specimen of *Kenyapithecus africanus* has only a slight lingual and mesial cingulum on its P⁴ and M¹, but material described more recently by Pickford (1982) from Majiwa includes some upper teeth with at least as great a cingulum development as on the Ad Dabtiyah specimens.

Our reason for interpreting premolar cusp heteromorphy and presence of cingula as primitive in this instance is the widespread occurrence of these characters in earlier Miocene and Oligocene hominoids and catarrhines. Neither character is present throughout the living catarrhines, and on this basis their absence would appear more likely to be primitive for this group. In this case, however, we feel that the fossil evidence can add to the evidence of living forms and suggest the alternative interpretation. Cusp heteromorphy and cingula are ubiquitous among early catarrhines like *Propliopithecus* (including *Aegyptopithecus*), *Dendropithecus*, *Micropithecus* and *Limnopithecus*; they are also present on early Miocene hominoids like *Proconsul* and *Rangwapithecus*, and they are now seen to be present in *Heliopithecus* and *Kenyapithecus* of the early middle Miocene. It is not until later in the middle Miocene that hominoids lacking these characters first appear, such as *Dryopithecus* and *Sivapithecus*, and we consider these hominoids to be derived in this respect.

These morphological changes can be put into phylogenetic perspective as follows: the primitive hominoid condition is considered to include premolars that were small relative to molar size, were mesiodistally compressed and had heteromorphic cusps; upper molars and the fourth premolar had low rounded cusps and well-developed lingual and mesial cingula. *Kenyapithecus* and *Dryopithecus* differ from this condition in the enlargement of the premolars, loss of premolar cusp heteromorphy, and the partial reduction of the cingulum, which is not developed on most specimens. *Heliopithecus* is intermediate in these characters, retaining a greater degree of cusp heteromorphy and cingulum development than seen in *Kenyapithecus* and *Dryopithecus* but linked with them through premolar enlargement.

Enamel structure and thickness

It has been possible to examine the enamel of one of the specimens from Ad Dabtiyah. The isolated M³ (M.35146) is naturally fractured, and the fractured surface has been exploited to study enamel thickness and enamel microstructure. The naturally fractured face passing through the paracone revealed a nearly ideal plane of section which minimized obliquity (Martin 1983, 1985). The slightly ragged fracture was flattened by diamond polishing to facilitate enamel thickness measurements and to produce a relief-free surface for back scattered (high energy) electron imaging. The plane in which enamel thickness was measured is shown in Fig. 14. Although this does not correspond exactly with the buccolingual plane of section through the mesial cusps recommended by Martin (1983), it is clear that it approximates to a section passing through the maximum diameter of the dentine horns and should produce results little affected by obliquity of section and therefore comparable with those from sectioned teeth.

The enamel thickness was measured for a number of linear dimensions which have been used previously (Martin 1983). Linear enamel thickness over the tip of the paracone of the M³ is 1.0 mm, and lateral enamel thickness on the buccal cusp is 0.92 mm (average 0.96 mm). The breadth of the tooth across the cervix is 8.1 mm, approximately the size of a chimpanzee M³, and comparable mean dimensions for chimpanzee enamel thickness are 0.5 mm at the tip of the paracone and 0.7 mm laterally. The enamel of *Heliopithecus leakeyi* is thus considerably thicker in absolute terms than that of the chimpanzee.

An attempt was made to scale enamel thickness by comparing enamel and dentine areas (Martin 1983, 1985). The area of enamel visible in section (as shown in Fig. 14) was measured, and this was then divided by the length of the enamel dentine junction in the same section; this approximates to the dimension c/e of Martin (1983, 1985) for the whole tooth. This dimension, which is called the Average Enamel Thickness, was then scaled for body size using the area of

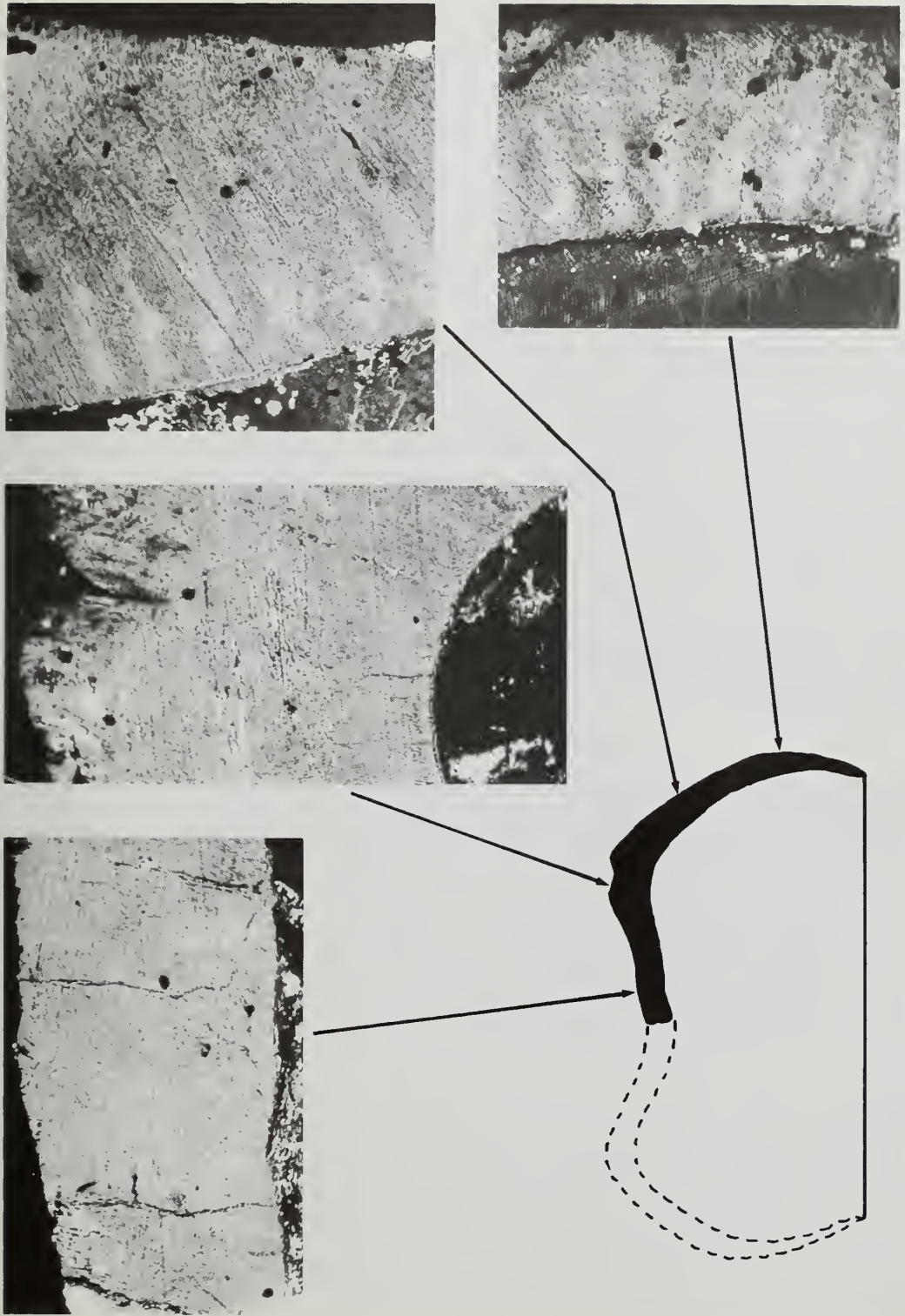


Fig. 14 Sections across the mesial face of the crown of the isolated M^3 (M.35146). The buccal half of the crown was broken when discovered and has been polished and etched to expose the prism structure and the enamel-dentine junction.

dentine in the same section (Martin 1983) as the estimator of body size. This gives the scaled dimension called the Relative Enamel Thickness, which in the case of the Ad Dabtiyah M³ has a value of 17.35. This compares with values of 8.90–11.30 for thin enamel (for instance in the chimpanzee and gorilla); 11.31–14.64 for intermediate/thin enamel; 14.65–17.49 for intermediate/thick enamel (as seen in the orang-utan); and 17.50–26.20 for thick enamel, which is seen in *Homo* and *Sivapithecus*. The enamel of *Heliopithecus* falls at the top end of the range of the intermediate/thick category, and although obliquity of section may have slightly increased the apparent enamel thickness, it is quite clear that *Heliopithecus leakeyi* has significantly thicker enamel than in chimpanzees, gorillas or gibbons, once size has been taken into account. Although the errors inherent in this estimation are recognized, we are confident that they have been reduced to a minimum and that *H. leakeyi* has enamel which is of intermediate thickness (as defined by Martin, 1985).

This result is significant in the light of the ancestral conditions for hominoid enamel determined by Martin (1985). The ancestral hominoid is thought to have had thin enamel, with thickened enamel as a derived character of the great ape and human clade. The presence of thickened enamel in *Heliopithecus* therefore represents a shared derived character with the great ape and human clade. Of the living members of this clade, only the orang-utan has enamel of intermediate thickness, and this might appear to be a point of resemblance to *H. leakeyi* in simple thickness terms. However, the enamel in the orang-utan is intermediate in thickness as a result of secondary reduction from thick enamel, while the enamel microstructure of *H. leakeyi* shows no such reduction, with the enamel being formed at a fast, pattern 3, rate throughout the enamel thickness. In *Pongo* the outer 20% of the enamel is formed at a reduced rate, as measured from prism cross-striation repeat intervals, but this is not the case in *H. leakeyi*. The enamel in *H. leakeyi* is of intermediate thickness in relation to the time available to develop enamel, and is not due to secondary reduction. As such it could represent an early stage in the evolution of thick enamel in the common ancestor of the great ape and human clade. It is interesting to note that this is the first evidence for intermediate-thickness enamel, all of which is fast-formed pattern 3 enamel, that has been seen in any hominoid species, these conditions having previously been predicted solely on the basis of end conditions of change (Martin 1983, 1985).

Phylogenetic interpretation

The new pieces of evidence presented here, from examination of the enamel and the reinterpretation of premolar and molar morphology, are consistent in their placement of *Heliopithecus leakeyi* in hominoid phylogeny. Premolar enlargement with retention of what are interpreted as ancestral characters, such as retention of molar cingula and premolar cusp heteromorphy, place *Heliopithecus* as an intermediate between the hominoid ancestral pattern and the great ape and human ancestral pattern which is shared also by *Kenyapithecus* and *Dryopithecus*. In other words, it is more closely related to the great apes and man than are the gibbons but less closely than are *Dryopithecus* and *Kenyapithecus*. The evidence from the enamel shows the same thing: the ancestral hominoid pattern is thin pattern 3 enamel such as is present in gibbons, while the ancestral great ape and man pattern is thick pattern 3 enamel which is retained unchanged in modern and fossil man; the intermediate thickness of enamel (all pattern 3) in *Heliopithecus* shows that it lacks the full development of this character, and our interpretation is that it is the sister group to the great ape and man clade, with some of its characters developed but not others.

These relationships are shown in Fig. 15. This shows *Proconsul* as the sister group to all other hominoids, living and fossil, and branching off before the divergence of the gibbons. After the gibbon divergence, first *Heliopithecus* and then *Kenyapithecus* diverged, so that both are successively sister groups to the living great apes and humans. The position of *Dryopithecus* with respect to *Kenyapithecus* is not certain. The basal split of the great ape and human clade is shown as that separating the orang-utan from the African apes and man (Andrews & Cronin 1982, Ward & Pilbeam 1983, Martin 1983), with the orang-utan joined with *Sivapithecus*. The remaining divergence is that between the African apes and man.

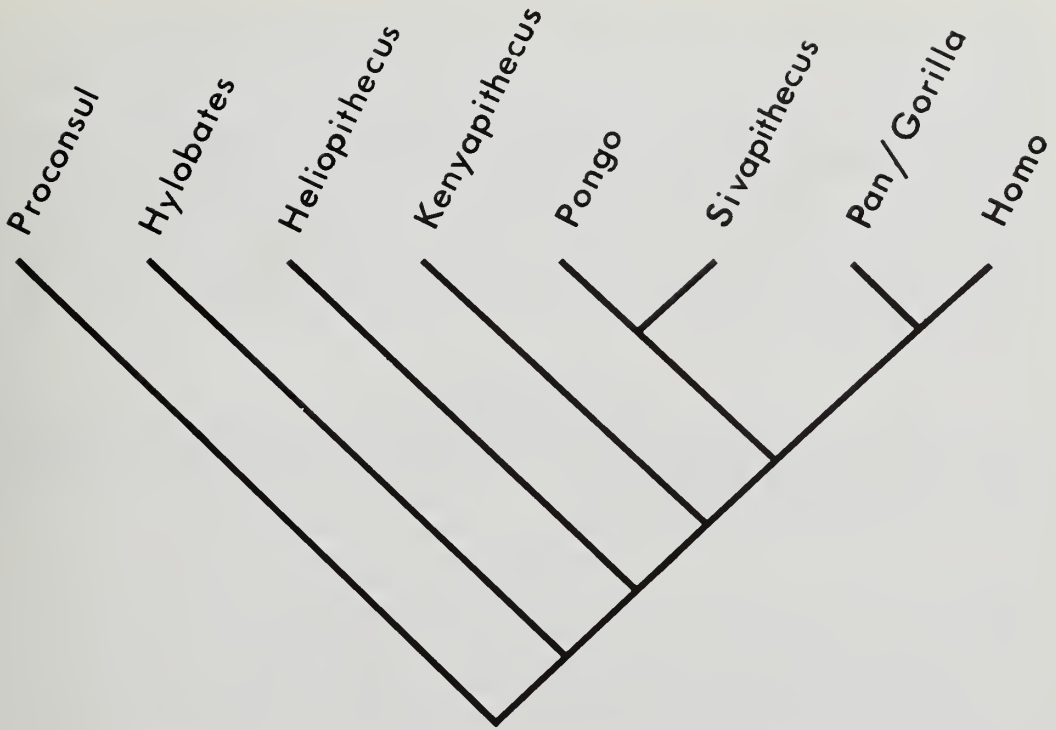


Fig. 15 Cladogram showing the proposed relationships of *Heliopithecus leakeyi*.

Note added in proof

Since this paper was submitted for publication in September 1984 new specimens have been found and named from East Africa (Leakey & Leakey 1986). We have not yet had the opportunity of making direct comparisons of *Heliopithecus leakeyi* with this new material, but the published descriptions and examination of casts indicates that there is a strong similarity between them.

The new material is from the site of Kalodirr west of Lake Turkana. It has been named *Afropithecus turkanensis* by R. E. and M. G. Leakey (1986) and the type specimen consists of a relatively complete skull with a number of unusual and rather baboon-like characters of the facial skeleton. In addition there are less complete specimens from the same site and from Buluk, east of Lake Turkana, which had been described in an earlier paper (Leakey & Walker 1985). The much less complete specimen from Ad Dabtiyah described here is not so well preserved as the East African material, but the parts that are preserved in common show a high degree of similarity.

Many characters of the *Afropithecus* specimens which are shared with other early Miocene and earlier fossil anthropoids would appear to represent primitive retentions for the Hominoidea. This applies to the wide interorbital distance, the massive glabellar region, the narrow and lightly built supraorbital tori not linking across the glabella, the oval-shaped nose, the nasal floor morphology, the single infra-orbital foramen, the relatively large lateral incisors compared with medial incisors, the heteromorphic premolars, and molars retaining distinct lingual cingula. These last two characters are seen to be present also in *Heliopithecus*, and the two genera also share the distinctive premolar enlargement described here. For example, the P^3/M^1 crown module ratio for *Afropithecus* is just over 100%, which is at the limits of the

gorilla range, and the P^4/M^1 ratio is 96%. In both cases the greatest similarities are with the Miocene genera *Heliopithecus* and *Kenyapithecus* together with the Moroto palate, which we have subsequently suggested represents a second species of *Heliopithecus* (Andrews, Martin & Whybrow 1987).

In terms of size, the *Afropithecus* specimens appear to group with the Moroto palate from Uganda and are considerably larger than *Heliopithecus* from Saudi Arabia. Because of this, there is little doubt about the species differentiation between the Saudi Arabian and African material, but it is unclear whether the generic distinction is justified. Without changing the main text of the present paper, we would like to place on record our doubts about the generic distinction. Additional material from Saudi Arabia providing data on the face of *Heliopithecus*, or information on the enamel structure and thickness of the teeth of *Afropithecus*, would either confirm or remove these doubts.

Acknowledgements

We are grateful to Peter Whybrow and Terry Harrison for comments on the text. Alan Boyde provided encouragement, support and SEM facilities for the enamel microstructure work. L.M. was supported by an MRC Research Training Fellowship and P.J.A. acknowledges funds from the British Council and the Wenner Gren Foundation for the work in Spain.

References

- Andrews, P. J. 1978. A revision of the Miocene Hominoidea of East Africa. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **30**: 85–224.
- 1985. Family group systematics and evolution among catarrhine primates. In: Delson, E. (ed.), *Ancestors: The Hard Evidence*: 14–32. New York.
- & Cronin, J. 1982. The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. *Nature, Lond.*, **297**: 541–546.
- , Hamilton, W. R. & Whybrow, P. J. 1978. Dryopithecines from the Miocene of Saudi Arabia. *Nature, Lond.*, **274**: 249–251.
- , Martin, L. & Whybrow, P. J. 1987. Earliest known member of the great ape and human clade. *Am. J. Phys. Anthropol.*, New York, **72**: 174–175.
- & Walker, A. C. 1976. The primate and other fauna from Fort Ternan, Kenya. In: Isaac, G. & McCown, E. R., (eds), *Human Origins*: 279–304. Menlo Park.
- Fleagle, J. E. 1986. The fossil record of early catarrhine evolution. In: Wood, B. A., Martin, L. B. & Andrews, P. J. (eds), *Major Topics in Primate and Human Evolution*: 130–149. Cambridge.
- Greenfield, L. O. 1979. On the adaptive pattern of 'Ramapithecus'. *Am. J. phys. Anthropol.*, Philadelphia, **50**: 527–548.
- 1980. A late divergence hypothesis. *Am. J. phys. Anthropol.*, New York, **52**: 351–365.
- Hamilton, W. R., Whybrow, P. J. & McClure, H. A. 1978. Fauna of fossil mammals from the Miocene of Saudi Arabia. *Nature, Lond.*, **274**: 248–249.
- Harrison, T. (1982.) *Small-bodied apes from the Miocene of East Africa*. 647 pp., 103 figs. Ph.D. thesis, Univ. London (unpubl.).
- Ishida, H., Pickford, M., Nakaya, H. & Nakano, Y. 1984. Fossil anthropoids from Nachola and Samburu Hills, Samburu District, Kenya. *Afr. Stud. Monogr.*, Kyoto, (suppl.) **2**: 73–85.
- Leakey, L. S. B. 1967. An early Miocene member of Hominidae. *Nature, Lond.*, **213**: 155–163.
- Leakey, R. E. & Leakey, M. B. 1986. A new Miocene hominoid from Kenya. *Nature, Lond.*, **324**: 143–146.
- & Walker, A. C. 1985. New higher primates from the early Miocene of Buluk, Kenya. *Nature, Lond.*, **318**: 173–175.
- Le Gros Clark, W. E. & Leakey, L. S. B. 1950. Diagnoses of East African Miocene Hominoidea. *Q. Jl geol. Soc. Lond.*, **105**: 260–262.
- Martin, L. B. (1983.) *The Relationships of the Later Miocene Hominoidea*. 450 pp., 50 figs. Ph.D. thesis, Univ. London (unpubl.).
- 1985. Significance of enamel thickness in hominoid evolution. *Nature, Lond.*, **314**: 260–263.
- 1986. Relationships among extant and extinct great apes and humans. In: Wood, B. A., Martin, L. B. & Andrews, P. J. (eds), *Major Topics in Primate and Human Evolution*: 161–187. Cambridge.
- & Andrews, P. J. 1982. New ideas on the relationships of the Miocene hominoids. *Primate Eye*, Cambridge, **18**: 4–7.

- Pickford, M.** 1982. New higher primate fossils from the middle Miocene deposits at Majiwa and Kaloma, Western Kenya. *Am. J. phys. Anthrop.*, New York, **58**: 1-19.
- Pilbeam, D. R.** 1969. Tertiary Pongidae of East Africa: evolutionary relationships and taxonomy. *Bull. Peabody Mus. nat. Hist.*, New Haven, **31**: 1-185.
- Simpson, G. G.** 1931. A new classification of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **59**: 259-293.
- Ward, S. C. & Pilbeam, D. R.** 1983. Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In: Ciochon, R. L. & Corruccini, R. S. (eds), *New Interpretations of Ape and Human Ancestry*: 211-238. New York.